

deutlichen Aufteilung innerhalb des gemeinsamen Verbreitungsgebietes. Auch in ihrer Ethologie und in der Aktivitätsperiodik gibt es einige weitere auffallende Unterschiede. Es werden Ergebnisse einer siebenmonatigen vergleichenden Untersuchung der zwei Dsungarischen Zwerghamster (*Phodopus sungorus sungorus* Pallas, 1770, und *Phodopus sungorus campbelli* Thomas, 1905) mit dem Roborowski-Zwerghamster (*Phodopus roborowskii* Satunin, 1903) vorgestellt. Bei letzterem wurde in einer sechzehnmonatigen Aktivitätsstudie ein äußerst markantes Aktivitätsminimum im Februar/März mit einer durchschnittlichen täglichen Laufaktivität von weniger als 10 Minuten nachgewiesen. Der sympatrisch vorkommende Dsungarische Zwerghamster *Phodopus sungorus campbelli* hat gerade in dieser Zeit ein Aktivitätsmaximum mit einer täglichen Laufaktivität (im Monatsmittel) von mehr als sechseinhalb Stunden. Beim Vergleich der allopatrischen Arten *Phodopus roborowskii* und *Phodopus sungorus sungorus* ist der Kurvenverlauf nahezu parallel.

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Size variation in cohorts of the Bank vole, *Clethrionomys glareolus* (Schreber, 1780), in Northern Finland

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Abstract

Studied size variation in the bank vole, *Clethrionomys glareolus* (Schreber, 1780) in three localities during different phases of population fluctuation. The 1424 specimens were obtained from trappings carried out once a month in 1966–72. The average size decreased in winter, but no clear trend was found in the size variation in the males and females, though there were some significant differences between them. The pregnant females from the autumn cohort were significantly longer in spring (III–V) than the non-pregnant ones, but this difference had disappeared by the summer (VI–VIII). A 3-year population rhythm was found at the three trapping localities. The voles born during the increase phase were larger than those born during the other phases in both cohorts until the spring. The differences between the voles from the different phases were more significant in the autumn cohort than in the spring cohort. Size was thus found to be connected with sex, age class and the phase of population fluctuation.

Introduction

Studies concerning the size and growth of the bank vole, *Clethrionomys glareolus* (Schreber, 1780), have shown that birth time has a great influence on growth (WASILEWSKI 1952; KUBIK 1965; BUJALSKA and GLIWICZ 1968; CRAWLEY 1970; ZEJDA 1971; KAIKUSALO 1972; WIGER 1979). The mean body size in a bank vole population diminishes in winter (HAITLINGER 1965; GRUBER and KAHMANN 1968; HYVÄRINEN and HEIKURA 1971; KAIKUSALO 1972). Sex-related size differences have been mentioned in some studies (STEIN 1956; HAITLINGER 1965), but no differences are recorded in the papers of BUJALSKA and GLIWICZ (1968) and KAIKUSALO (1972).

Bank vole populations fluctuate in the northern parts of the distribution area, with the phase of fluctuation affecting body size (HANSSON 1969).

The aim of this work is to explain the influence of factors such as season, sex, age class, trapping site and phase of population fluctuation on the size of the bank vole, and to study growth in bank voles on the basis of accurate determinations of age and regular monthly trapping results. The material permitted the above data to be examined over an extended period of time in the northern part of the distribution area of this species, where its population fluctuations are clear.

Material and methods

The material consists of bank voles trapped by the Department of Zoology at the University of Oulu from October 1966 to September 1972. The trapping sites were chosen from the same latitude, as follows: Tupos (Kempele) 64° 55' N: 25° 30' E, Muhos 64° 50' N: 26° 05' E and Paljakka (Hyrynsalmi) 64° 40' N: 28° 05' E. Two biotopes were chosen at each locality: a spruce forest and abandoned field. At Tupos and Muhos the field was an open area, but at Paljakka it comprised the banks of ditches and partially overgrown forest clearings. Paljakka also differs from the other sites in having a thicker snow cover (VIRO 1974a).

The trappings were carried out once a month for one night at each locality, involving 100 traps both in the forest and in the fields (for details, see HYVÄRINEN and HEIKURA 1971). 1424 specimens were obtained in all. The numbers of specimens measured are given in Table 1.

The bank voles were weighed and their length from the tip of the snout to the anus was measured (SIIVONEN 1977). Age determination was based on the length of the roots of the first mandibular molar (VIRO 1974b).

The material was classified into two age classes or cohorts, those born before July being placed in the spring cohort (C₁) and those born during or after July in the autumn cohort (C₂).

Table 1

Numbers of bank vole specimens measured

	Tupos		Muhos		Paljakka		Σ
	Forest	Fields	Forest	Fields	Forest	Fields	
Weight							
♂♂	172	43	117	20	159	176	
non-pregnant ♀♀	132	41	129	13	132	126	
pregnant ♀♀	15	2	16	0	16	22	
Σ	319	86	322	33	307	324	1391
Length							
♂♂	146	40	160	19	133	164	
non-pregnant ♀♀	107	39	114	12	106	113	
pregnant ♀♀	12	2	13	0	16	20	
Σ	265	81	287	31	255	297	1216

Table 2

Statistically significant differences in body weight and length in the bank voles between the cohorts
(excluding pregnant females)

	Males			Females			P
	\bar{x}	C ₁ S.D.	n	\bar{x}	C ₁ S.D.	n	
Body weight g							
Tupos							
1st autumn				16.8	3.20	20	<0.005
Muhos							
1st autumn				18.8	2.01	12	<0.001
1st winter				18.4	1.08	3	<0.001
Palj akka							
1st autumn	16.1	1.33	12	18.2	2.67	21	<0.005
2nd summer	24.8	1.33	12				<0.001
Body length mm							
Tupos							
1st autumn				91.2	3.82	15	<0.005
Muhos							
1st autumn	92.1	4.03	11	95.3	4.63	12	<0.05
1st winter				98.4	3.09	3	<0.001
Palj akka							
1st autumn	90.5	3.76	11	95.9	5.35	18	<0.05
				87.0	4.16	79	<0.001

C₁ = spring cohort, C₂ = autumn cohort. Summer = June–August, autumn = September–November, winter = December–February, spring = March–May.

Since the number and size of the embryos have a decisive influence on the total weight of a pregnant female, embryos longer than 5 mm have to be taken into account when measuring the body weights of females (MAZÁK 1962). Consequently all the visibly pregnant females (72 individuals) were excluded from the calculations of mean weights. The lengths of the visibly pregnant females were also treated separately because of the importance of maintaining homogeneity in the material. The lactating females were included with the other female voles.

Each trapping site showed a 3-year rhythm of population fluctuation during the period studied. This was synchronized at Tupos and Muhos, but delayed by one year at Paljakka. At Muhos the peak was so unclear (VIRO 1974a) that the material was omitted from the present comparison.

The material was analysed by taking the specimens born in the peak year as a single group, which was then traced through to the following crash year. The specimens born during the crash and increasing years were then dealt with in the same way.

Results

Seasonal variation in body size

The bank voles varied in weight and length according to season in a different manner in each age class (Figs. 1 and 2, Table 2). Those born in the first half of the summer (C_1) had grown a little by the autumn, but their mean length seemed to diminish in winter, while the

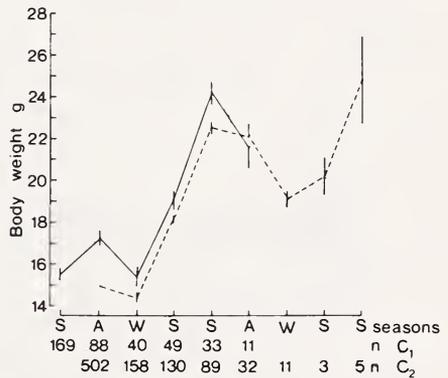
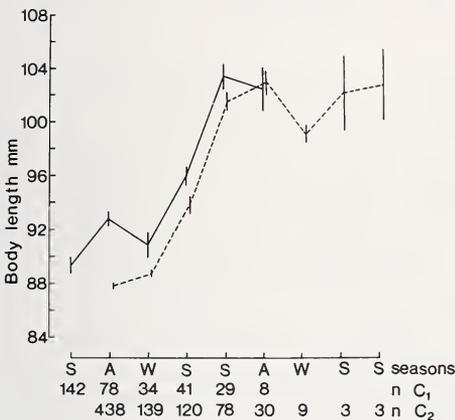


Fig. 1. Seasonal variation in mean body length in the bank voles (excluding pregnant females). Symbols: — = C_1 , --- = C_2 . Vertical lines represent one standard error on either side of the mean

Fig. 2. Seasonal variation in mean body weight in the bank voles (excluding pregnant females). Symbols: — = C_1 , --- = C_2 . Vertical lines represent one standard error on one side of the mean

Table 3

Body length in the bank voles in autumn and winter (excluding pregnant females)

		\bar{x}	S.D.	n	p
C_1	1st autumn	92.8	4.81	78	< 0.05
	1st winter	90.6	5.46	34	
C_2	1st autumn	87.8	4.34	438	< 0.001
	1st winter	88.6	3.57	139	
	2nd autumn	102.8	4.96	39	
	2nd winter	98.8	2.18	9	

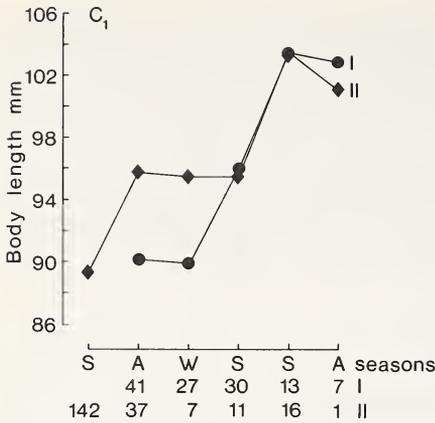


Fig. 3. Seasonal variation in mean body length in the bank voles of the spring cohort (C_1), excluding pregnant females. Symbols: ●—● = younger age group, ◆—◆ = older age group

mean length of the autumn cohort (C_2) did not diminish until the second winter (Fig. 1, Table 3), when about 2% of the specimens from the first autumn were still alive. The voles belonging to the autumn cohort were shorter than those belonging to the spring cohort in their first autumn (Table 3).

In the C_1 there was a difference of five months between the youngest and oldest individuals in every season, and consequently this cohort was divided further into two age groups and the length variations in these studied separately (Fig. 3, Table 4). Since the younger age group accounted for nearly 53% of this cohort in autumn and 79% in winter, their small size served to reduce the mean length of C_1 . There was no corresponding difference in mean length in C_2 even though the age range inside the age class was more than five months.

Table 4

Body length in the bank voles of C_1 in autumn and winter

	\bar{x}	S.D.	n	p
Autumn				
older age group	95.6	4.72	37	< 0.001
younger age group	90.3	3.30	41	
Winter				
older age group	95.4	6.23	7	< 0.01
younger age group	89.4	4.58	27	

Older age group = individuals born in April–May, younger age group = individuals born in June.

Growth was vigorous in spring, and the voles reached a mean length of 103.4 ± 0.83 mm in the summer (Fig. 1). The animals in the two cohorts grew differently in spring, however, the C_1 individuals at Paljakka diminishing in weight from March to May and in length from April to May, the same also being seen separately in the males and females, whereas the C_2 specimens increased steadily in weight and length during the spring at every trapping site.

Size variation among pregnant and lactating females

The visibly pregnant females in the spring cohort at Paljakka were significantly longer in summer than the non-pregnant ones ($t = 2.179$, $p < 0.05$), as also were the pregnant females of the autumn cohort in spring at Muhos ($t = 4.173$, $p < 0.005$) and at Paljakka ($t = 2.883$, $p < 0.01$). The trend was similar at Tupos, but the difference was not statistically significant (Fig. 4).

The lactating females were heavier and longer than other non-pregnant females at the same period (summer and autumn) (Table 5).

Table 5

Body weight and length in the female bank voles in summer and autumn (excluding pregnant females)

	\bar{x}	S.D.	n	p
Weight (g)				
lactating	22.6	3.62	16	
non-lactating	16.0	3.94	352	<0.001
Length (mm)				
lactating	98.7	3.77	13	
non-lactating	89.3	7.45	301	<0.001

Fig. 4. Seasonal variation in mean body length in the female bank voles. Symbols: ○---○ = pregnant, ●---● = non-pregnant. Vertical lines represent one standard error on one side of the mean. The asterisks represent statistical significance

Size variation between trapping sites

There was some variation in size between the voles caught at the three trapping localities, with those from Tupos in the first autumn smaller than the others (in C₁ $t = 2.704$, $df = 76$, $p < 0.005$ and in C₂ $t = 1.966$, $df = 436$, $p < 0.05$).

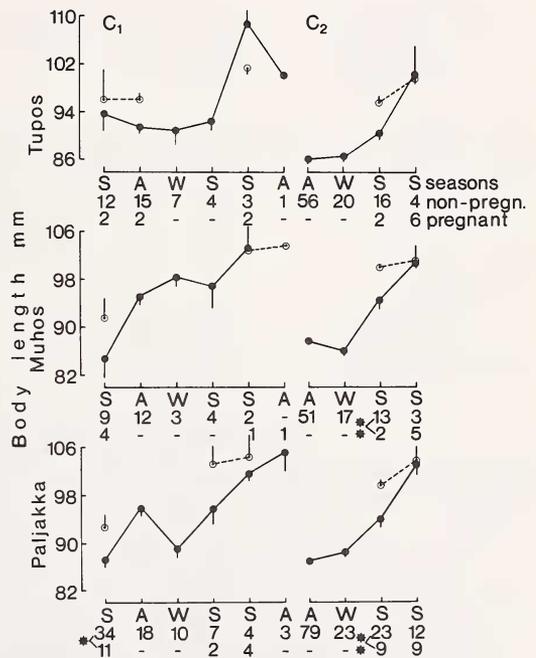
Body size was similar in both biotopes in all cases except the C₂ females at Paljakka in spring, where the females were heavier in the fields than in the forest (fields: $\bar{x} = 20.5$ g, S.D. = 4.19, $n = 9$ and forest: $\bar{x} = 15.9$ g, S.D. = 2.04, $n = 18$; $t = 3.148$, $p < 0.025$). This shows that the field area at Paljakka provides good living conditions, as reflected in the number of specimens captured (Table 1).

Because of the great similarity in the body size between the forest and field areas, the catches from the two biotopes are combined in the following chapters.

Size variation between cohorts and sexes

The differences in size between the cohorts were apparent before wintering (Figs. 1 and 2). In the first autumn of their lifespan the C₁ specimens were significantly longer than those in C₂ (Table 2), a corresponding difference in weight being seen at Tupos and Muhos only among the females. In winter the differences disappeared, while at Paljakka the C₁ males remained heavier than those of C₂ even after wintering.

Significant differences in size between the sexes were found irregularly at different



trapping sites and in different seasons, but the females were most often heavier, whereas the males were characteristically longer (Table 6). Since the differences between the sexes were small and irregular, the males and females were combined.

Table 6

Statistically significant differences in body weight and body length between the male and non-pregnant female bank voles

	Males			Females			p
	\bar{x}	S.D.	n	\bar{x}	S.D.	n	
Body weight g							
Muhos							
C ₂ 1st winter	15.2	1.51	16	14.0	1.30	24	<0.025
Paljakka							
C ₁ 1st autumn	16.1	1.33	12	18.2	2.67	21	<0.01
C ₂ 2nd summer	21.8	2.35	34	24.9	4.11	14	<0.025
2nd autumn	20.2	1.07	5	22.7	1.57	3	<0.05
Body length mm							
Tupos							
C ₂ 1st winter	89.3	2.12	23	86.6	3.74	20	<0.01
Muhos							
C ₂ 1st autumn	89.4	3.63	73	87.9	4.34	51	<0.05
1st winter	90.2	3.74	17	86.1	3.50	17	<0.005
Paljakka							
C ₁ 1st summer	90.8	7.01	51	87.4	7.74	34	<0.05
1st autumn	90.5	3.76	11	95.9	5.35	18	<0.01
C ₂ 2nd autumn	100.5	3.50	5	106.4	2.34	3	<0.05

Size variation during population fluctuation

The voles born during the increasing year were heavier in winter only in C₁ at Paljakka compared with those born during the peak year (Fig. 5, Table 7).

There were more differences between the fluctuation phases in the autumn cohort than in the spring cohort (Figs. 5 and 6, Table 7). At Tupos the voles born during the increasing year and still alive in the peak year, were the heaviest through to the spring. The size relationships at Paljakka were similar, but not as clear, those born during the increasing year being the largest and those from the low year the smallest.

The weight of the wintered males was greater during the peak phase than during the low phase of the fluctuation (Fig. 7), the mean being 23.3 g (S.D. = 2.09, n = 37) at the peak and 20.7 g (S.D. = 2.07, n = 24) in the low phase. The difference was highly significant (t = 4.896, p < 0.001).

The wintered males did not differ in length from one phase of fluctuation to another (peak: \bar{x} = 102.3 mm, S.D. = 4.93, n = 34; low phase: \bar{x} = 101.1 mm, S.D. = 4.97, n = 22).

Discussion

Seasonal variation in size

The mean length and weight of the bank voles diminished in winter. A smaller size would be more economical on energy in winter (KALELA 1957; IVERSON and TURNER 1974; BEACHAM 1980), but because of the limitations in this material the individual reduction of

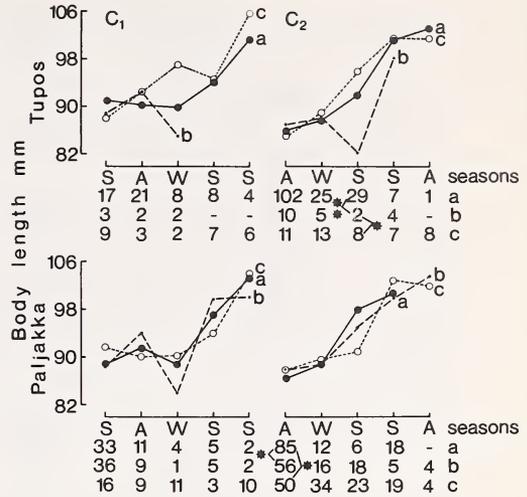
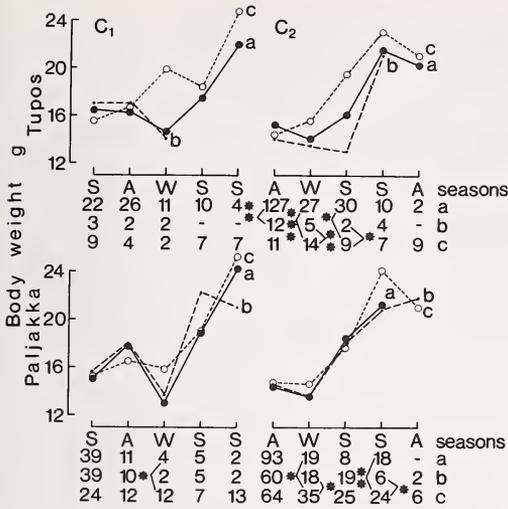


Fig. 5. Seasonal variation in mean body weight in the bank voles (excluding pregnant females) during the different phases of population fluctuation. Symbols: a, ●—● = born during peak years, b, ●---● = born during decreasing years, c, ○--○ = born during increasing years. The asterisks represent statistical significance

Fig. 6. Seasonal variation in mean body length in the bank voles (excluding pregnant females) during the different phases of population fluctuation. Symbols as in Fig. 5

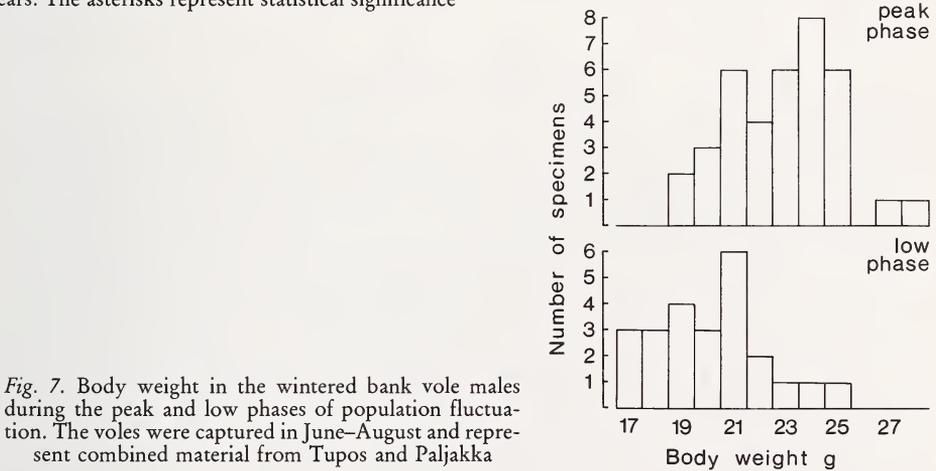


Fig. 7. Body weight in the wintered bank vole males during the peak and low phases of population fluctuation. The voles were captured in June–August and represent combined material from Tupos and Paljakka

weight cannot be proved. On the other hand, weight may diminish only in one age class (ZEJDA 1971) or only during certain phases of the population fluctuation (BEACHAM 1980). It is obvious that at least this has some influence on the winter reduction in body weight. The loss in weight is clearer here in C₁, but can be detected in both cohorts. Declines in mean weight in the bank vole in winter are also mentioned by HAITLINGER (1965), ZEJDA (1971) and KAIKUSALO (1972), and the same phenomenon is also encountered in other microtines, e.g. *Clethrionomys rufocanus* (KALELA 1957), *Microtus pennsylvanicus* (IVERSON and TURNER 1974), *M. oeconomus* (WHITNEY 1976) and *M. townsendii* (BEACHAM 1980).

Enzyme activity in the bones of the bank vole is low in winter, (HYVÄRINEN 1969a; HYVÄRINEN and HEIKURA 1971), which should explain the cessation in growth. In the

Table 7

Statistically significant differences in body weight and body length between the three phases of the population cycle

	A		Differences between A and B		B		Differences between B and C		C		Differences between A and C	P
	\bar{x}	S.D.	n	P	\bar{x}	S.D.	n	P	\bar{x}	S.D.		
Body weight g												
Tupos												
C ₂ 1st autumn	15.1	1.76	127	<0.005	14.1	0.73	12		16.7	1.74	14	<0.001
1st winter	13.9	1.11	27		13.6	1.41	5	<0.005	19.3	3.65	9	<0.05
1st spring	16.0	3.98	30		12.9	0.78	2	<0.05				
Paljakka												
C ₁ 1st winter	13.0	1.81	4						15.7	1.64	12	<0.025
C ₂ 1st winter	13.7	1.23	19		13.7	1.33	18	<0.05	14.6	1.50	35	<0.05
2nd summer	21.4	2.45	18		21.0	2.68	6	<0.05	24.2	3.17	24	<0.005
Body length mm												
Tupos												
C ₂ 1st spring	92.0	4.55	29	<0.01	82.2	2.33	2	<0.05	96.2	7.99	8	
Paljakka												
C ₂ 1st autumn	86.7	3.90	85	<0.025	88.3	3.84	56		88.2	3.79	50	<0.05

A = Born during the peak phase, B = born during the low phase, C = born during the increasing phase. The curves for body weight are given in Fig. 5 and those for body length in Fig. 6.

shrew, the skeleton is even reduced in size in winter through diminution of the intervertebral discs and cartilage (HYVÄRINEN 1969b), and the skull of the bank vole similarly shrinks in winter (HAITLINGER 1965).

A cessation in growth is also noted by ZEJDA (1971) and KAIKUSALO (1972). The winter decline in the mean length of a bank vole population is explained by HAITLINGER (1965) as being due to those juveniles born in the second half of the breeding season, which grow slowly.

The same phenomenon could also be seen in this material if cohorts were combined, but here the voles of C_1 "diminish" in length, too. In ZEJDA's (1971) material the mean length decreases in the first of the three cohorts, because about half of the individuals in this cohort die in the autumn, and particularly the longest ones. The same has been noted in *M. oeconomus* (MARKOWSKI 1980). Division of the present C_1 into two age groups shows that the youngest voles remain the smallest in winter and serve to reduce the mean length of their great number. Thus no real shrinking of the skeleton is needed to explain the decline.

The onset of growth in spring occurs in March, as has also been observed to be case in Southern Sweden (BERGSTEDT 1965), Poland (HAITLINGER 1965) and England (CRAWLEY 1970).

The voles belonging to C_1 at Paljakka form an exception to the normal spring growth model. Here the largest animals, which cause the clear peak in March, belong to the material from 1969, which represents an increasing phase. The only winter pregnancies in the whole material are from the same year and month.

The fact that large individuals mature earlier than small ones (MARKOWSKI 1980) is observed in this study at Paljakka in winter 1969 and in the females of C_1 in the spring.

Size variation by cohort and sex

The juvenile bank voles born in autumn are smaller than those born in spring or summer (MAZÁK 1962), and their growth rate is slower than in those born in spring (WASILEWSKI 1952; HAITLINGER 1965; KUBIK 1965; BERGSTEDT 1965; CRAWLEY 1970; ZEJDA 1971).

Size differences between the cohorts are seen in the present material before wintering, when the voles in C_1 are bigger, but this normally disappears after wintering, except in one case, at Paljakka in spring, where the males were heavier in C_1 than in C_2 . This is connected with the exceptional size development of the voles at Paljakka. On the other hand, the identical growth rates reported for voles born in cold seasons, i.e. spring and autumn (SVIRIDENKO 1959; BUJALSKA and GLIWICZ 1968) cannot be seen in this material. One reason for this may be the short breeding period, so that only two cohorts exist.

The differential growth rate is connected with differences in physiological maturation in rodents (SCHWARZ et al. 1964). In bank voles the individuals in the autumn cohort are physiologically younger than those of the same age born earlier in the breeding season (FEDYK 1974), and they also survive best in winter (WIGER 1979). Some individuals of C_2 even live over the second winter of their lifespan, having been born outside the normal breeding period (cf. pregnant females in March 1969) and thus having in a way lived through only one and a half winters.

Differences in size occurred between the males and females at all seasons except in spring, at all the trapping sites and in both cohorts, the longer specimens being mostly males and the heavier ones females. There are some bank vole populations, however, in which no sex-related variations in body size have been noted (HAITLINGER 1965; BUJALSKA and GLIWICZ 1968; ZEJDA 1971; KAIKUSALO 1972).

In spring the C_2 pregnant females are longer than the non-pregnant ones, which are still growing. ZEJDA (1967) also notes that the pregnant females grow at the beginning of the breeding season, at a time when the males no longer increase in weight at all.

Size variation during population fluctuations

Various strategies have been put forward to explain the correlation between mean size and the fluctuation phases of a population. K or α -strategists (i.e. slow maturation, large size) are predominant during the peak phases and r-strategists (i.e. early maturation, small size) dominate during the increasing phases (see MACARTHUR and WILSON 1967; PIANKA 1970; STENSETH 1978; WIGER 1979; BEACHAM and KREBS 1980). The existence of genetically selected phenotypes is regarded as the basis for these two strategic models noted in Microtinae populations (see CHITTY 1960; BOONSTRA and KREBS 1979). WIGER (1982), however, in his study concerning *Clethrionomys* species, concludes that there could be some response by the individuals to changes in their social environment.

The existence of large individuals during peak population phases is known in many fluctuating species, both in the genus *Microtus* (CHITTY 1952; BOONSTRA and KREBS 1979; BEACHAM 1980) and in the genus *Clethrionomys* (STEIN 1956; HANSSON 1969; WHITNEY 1976; WIGER 1979, 1982), although exceptional populations have also been described (*C. rutilus* and *C. gapperi* FULLER 1969). Large individuals are found at the peak phase in this material in some cases, the wintered males in June (i.e. those born during the increasing phase) being the heaviest during the peak phases. Similar results have been obtained from data on bank vole populations in Northern Sweden (GUSTAFSSON, pers. comm.).

The weight of the males after wintering is lowest in the years with low numbers, as was also found by HANSSON (1969). This is in contradiction to the situation in the total material of this study, where the C_2 voles born during the low phases are the smallest and weakest. By winter these count as belonging to the increasing phase, in which small size has been noted in some other Microtinae populations (WIGER 1979; BEACHAM and KREBS 1980). A rapid growth rate (KREBS et al. 1973; FULLER 1977; BEACHAM 1980), good condition (HEIKURA 1977) and early maturation in the increasing phase (WIGER 1979; BEACHAM and KREBS 1980) have also been observed in some Microtinae species.

This material makes it possible to follow the trends in body size in successive seasons and phases. It is obvious that the selection of the material has an important influence on the results concerning the relation between body size and the phase of population fluctuation.

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Zusammenfassung

Größenschwankungen bei der Rötelmaus Clethrionomys glareolus (Schreber, 1780) in verschiedenen Altersklassen, untersucht in Nordfinnland

Die Größenschwankungen bei der Rötelmaus *Clethrionomys glareolus* wurden in drei Gebieten während verschiedener Stadien der Populationsdichte untersucht. Das Untersuchungsmaterial stammt aus Fängen der Jahre 1966–1972. Die mittlere Größe nahm während des Winters ab. Ein deutlicher Zusammenhang zwischen Schwankungen in der Größe einerseits und dem Geschlecht andererseits konnte nicht nachgewiesen werden, obwohl es in einigen Fällen erhebliche Unterschiede zwischen den Geschlechtern gab. Die im Herbst geborenen tragenden Weibchen waren im Frühjahr (III–V) erheblich länger als die nichttragenden. Dieser Unterschied verschwand bis zum Beginn des Sommers (VI–VIII). Eine Fluktuation der Bestandsdichte im 3-Jahres-Zyklus wurde an allen drei Fangplätzen festgestellt. Die Rötelmäuse, die in einer Anstiegsphase geboren wurden, waren größer als die, die nicht in einer solchen Phase geboren wurden. Die Unterschiede der in den verschiedenen Zyklen geborenen Rötelmäuse waren bei den im Herbst geborenen deutlicher als bei den im Frühjahr geborenen. Es wurde festgestellt, daß die Größe der Rötelmaus mit dem Geschlecht, der Altersklasse und dem Zyklus der fluktuierenden Bestandsdichte in Zusammenhang steht.

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Gastrointestinal anatomy of the European badger *Meles meles* L. A comparative study

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Abstract

The gastrointestinal tract of the European badger (*Meles meles* L.) consists of a simple elongated stomach, tortuous small intestine and simple smooth-walled colon. There is no caecum. Allometric comparison of the internal surface area of the main gut compartments with comparable data from a variety of mammal species shows that the badger has a marginally larger stomach, larger small intestine and smaller colon than expected for its body weight. Multivariate analysis based on the absorptive areas of the three main gut compartments, taking into account body size, places the badger close to other mustelids and within a cluster of species most of whose diets are faunivorous.

Introduction

KRUUK (1978a, b; KRUUK et al. 1979; KRUUK and PARISH 1981) has characterised the European badger as a specialist predator on earthworms, especially *Lumbricus terrestris*. Stomach contents and faeces of badgers from Osefordshire and Scotland reveal a high incidence of earthworm remains, while behavioural observations suggest not only that badgers spend most of their foraging time looking for and consuming worms, but also that wormhunting effort increases or decreases to compensate for changes in prey availability.